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Impact of root system architecture on rhizosphere and root microbiome

Muhammad Saleem[a,*], Audrey D. Law[a], Mohammad Radhi Sahib[b,e], Zahida H. Pervaiz[c], Qingming Zhang[a,d]

[a] Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY, USA
[b] Department of Horticulture, University of Kentucky, Lexington, KY 40546-0312, USA
[c] Department of Veterinary Science, University of Kentucky, Lexington, KY 40546-0312, USA
[d] College of Plant Health and Medicine, Qingdao Agricultural University, Qingdao 266109, China
[e] Al Qasim Green University, Babylon, Iraq

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ABSTRACT

The root system influences plant fitness, health, and productivity via its phenotypic traits (phenes) such as root length, biomass, density, volume, and surface area. Although these traits differentially impact the release of 20 to 80% of total photosynthates as root exudates, their role in influencing microbial communities in the rhizosphere and root environments is not clear. The root phenes or architecture significantly alter soil biophysical and edaphic properties such as aggregation, structure, pH, moisture, temperature, and nutrient stoichiometry (C:N, C:P, and N:P ratios, etc.). Meantime, the exteriors and interiors of various root types demonstrate a tremendous phenotypic plasticity in their cellular structure, anatomy, cell types, shapes, metabolisms and biochemical profiles. These heterogeneities in the rhizosphere and endosphere create micro-environments and ecological niches for diverse microbial species to foster beneficial rhizospheric interactions. Results from the root systems of some agricultural, forest and model plants suggest that root phenes selectively filter and recruit different microbial communities. However, microbial colonization of root and rhizosphere environments may also occur through vertical transmission. We suggest that plant breeders should nevertheless consider root phenome and biota while developing new cultivars. Linking root phenome to microbiome (or its functional traits) and crop management practices may enhance our understanding of rhizospheric interactions, and their role in developing climate-resilient rhizosphere ecosystems.

1. Introduction

The plant-microbe interactions either above- or belowground significantly impact microbial community structure and plant performance (Saleem et al., 2017; Saleem and Moe, 2014; Zhang et al., 2017). The rhizosphere, a belowground root-affected soil portion, is inhabited by highly diverse communities of macro-and microorganisms that deliver essential ecosystem services such as nutrient cycling, soil structuring, stress alleviation, resource use efficiency, carbon sequestration, and biodegradation of the contaminants (Saleem, 2015; Saleem and Moe, 2014). While the root system impacts plant growth by physical support, nutrient foraging, gaseous exchange and recruiting beneficial microbes (Bardgett et al., 2014). The root phenes that include but are not limited to these; root branches, length, biomass, volume, anatomy, and surface area (Lynch and Brown, 2012), etc., enable plant survival under various biotic and abiotic stresses such as salinity, temperature extremes, waterlogging, drought, and nutrient shortage. Despite several studies on root-microbe interactions, we know little about the impact of root phenotypic traits on the root and rhizosphere microbial communities and their functions (but see, Szoboszlay et al., 2015) (Fig. 1).

1.1. Plant variety, root system, and microbial functional traits

There is an emerging interest in understanding the role of root and rhizosphere heterogeneities in structuring the microbial communities of these environments (Beckers et al., 2017; Saleem et al., 2018). Pérez-Jaramillo et al., (2017) compared the rhizosphere microbiome of wild and modern bean accessions. Both types of accessions differ in their root phenology. The wild and modern bean accessions have thin and thick roots, respectively. While profiling microbial communities, they showed a differential abundance of bacterial taxa (phyla, family, and OTU) in the rhizosphere of bean accessions. The *Bacteroidetes* as well as *Verrucomicrobia*, and *Actinobacteria* showed higher relative abundance in the rhizosphere microbiome of wild and modern bean accessions,

* Corresponding author.
E-mail address: m.saleem@uky.edu (M. Saleem).

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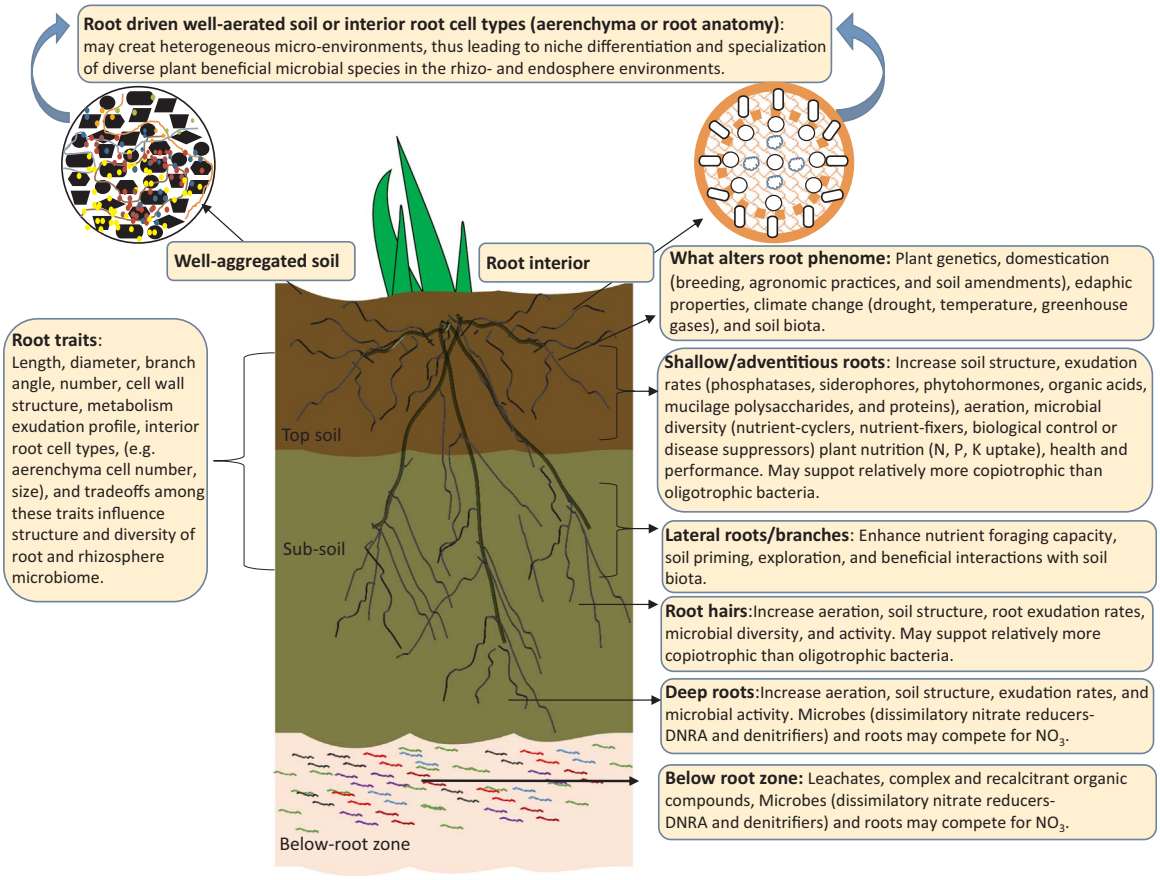
Root driven well-aerated soil or interior root cell types (aerenchyma or root anatomy): may creat heterogeneous micro-environments, thus leading to niche differentiation and specialization of diverse plant beneficial microbial species in the rhizo- and endosphere environments.
Well-aggregated soil
Root interior
What alters root phenome: Plant genetics, domestication (breeding, agronomic practices, and soil amendments), edaphic properties, climate change (drought, temperature, greenhouse gases), and soil biota.
Root traits: Length, diameter, branch angle, number, cell wall structure, metabolism exudation profile, interior root cell types, (e.g. aerenchyma cell number, size), and tradeoffs among these traits influence structure and diversity of root and rhizosphere microbiome.
Top soil
Sub-soil
Shallow/adventitious roots: Increase soil structure, exudation rates (phosphatases, siderophores, phytohormones, organic acids, mucilage polysaccharides, and proteins), aeration, microbial diversity (nutrient-cyclers, nutrient-fixers, biological control or disease suppressors) plant nutrition (N, P, K uptake), health and performance. May suppot relatively more copiotrophic than oligotrophic bacteria.
Lateral roots/branches: Enhance nutrient foraging capacity, soil priming, exploration, and beneficial interactions with soil biota.
Root hairs:Increase aeration, soil structure, root exudation rates, microbial diversity, and activity. May suppot relatively more copiotrophic than oligotrophic bacteria.
Deep roots:Increase aeration, soil structure, exudation rates, and microbial activity. Microbes (dissimilatory nitrate reducers-DNRA and denitrifiers) and roots may compete for NO_3.
Below root zone: Leachates, complex and recalcitrant organic compounds, Microbes (dissimilatory nitrate reducers-DNRA and denitrifiers) and roots may compete for NO_3.
Below-root zone

Fig. 1. The sketch of plant root system. The root system architecture (or root system) implies the spatial arrangement of seminal primary, secondary (lateral) and root hairs (fine roots) in the rhizosphere environment. It is an integral component of the plant that determines its survival and performance. Generally the plants with greater root density, biomass, length and branches could alter the rhizosphere environment in their favor, and thus are considered more productive under harsh environmental conditions. Since root system is comprised of numerous architectural and morphological traits, understanding the differences in microbial diversity across root traits is important to increase our understanding of rhizospheric interactions and their role in crop production.

respectively (Pérez-Jaramillo et al., 2017). While using two field grown nicotiana cultivars, we compared the abundance of bacterial taxa across the root phenotypic gradient (fine roots → secondary roots → primary roots) (Saleem et al., 2016). If the abundance of these OTUs does not and does change across this gradient, then these OTUs are named as generalist and specialist colonizers, respectively. The generalist pool consisted of OTUs, mainly from proteobacteria, including OTUs from other phyla as well. Nevertheless, the relative abundance of these generalists did differ in different plant cultivars. For instance, *Rhizobium* and *Pantoea* dominated the root (all phenotypic traits) microbiome of two commercial burley tobacco (*Nicotiana tabacum*) varieties such as KT204LC and NCBH129LC, respectively (Saleem et al., 2016). Overall, the generalist pool represented a tremendous diversity of OTUs that include but were not limited to these (top 10): *Rhizobium, Comamonadaceae, Aminobacter, Pantoea, Pseudomonas, Shinella, Rhizobiaceae, Sphingopyxis, Comamonadaceae*, and *Variovorax*, etc. Although less in numbers, the specialist root colonizers also belonged to several bacterial phyla. For instance, the OTUs from proteobacteria included: *Rhizobium*, *Sphingopyxis*, *Sphingomonadaceae*, *Sphingomonas, Burkholderiales,* and *Bradyrhizobiaceae*. Mostly, the abundance of specialist OTUs decreased from fine to primary roots depending on the crop cultivar (Fig. 2). However, the abundance of one OTU namely "*Sphingopyxis*" increased from root hairs to the primary roots in NCBH 129LC.The *Verrucomicrobia* OTUs were mostly specialists in the KT 204LC (Fig. 2). Notably, the abundance of two *Verrucomicrobia* OTUs increased and decreased across the root phenotypic gradient. Interestingly, the abundance of *Spartobacteria* decreased and increased across the root phenotypic gradient in NCBH 129LC and KT 204LC, respectively (Fig. 2) (Saleem et al., 2016). While the abundance of three *Actinobacteria* OTUs decreased from root hairs to the primary roots in the KT 204LC (Fig. 2). Conversely, the abundance of two *Bacteroidetes* OTUs increased whereas of one decreased across the phenotypic trait gradient (Saleem et al., 2016). Apart from these, there are some evidences that suggests preferential colonization of bacterial taxa at phyla (DeAngelis et al., 2009) and OTU level, on and inside (Marasco et al., 2012; Massalha et al., 2017) roots including root hairs (Mousa et al., 2016). However, we know little about the role of microbial biochemical (root cell wall degradation, metabolites consumption, etc.), ecological (species interactions such as competition, facilitations, antagonisms, etc.), and molecular traits (quorum-sensing signal) in the development of root phoneme-specific microbiome.

1.2. Generalist or specialist microbial partners: root phenes specificity

A greater abundance and diversity of generalists predict the potential of generalist taxa in occupying root phenotypic traits to exploit the surrounding ecological resources (i.e., metabolites, nutrients, etc.) (Bais et al., 2006; Marschner et al., 2001). Most of generalists taxa are known to impact plant growth under a broad range of environmental conditions (Egamberdieva et al., 2016; Rubin et al., 2017; Saleem et al., 2007; Zhang et al., 2017). Among root specialists, a majority of OTUs showed relatively high abundance in the fine roots that could be due to two reasons. First, the surface area of fine roots is much higher than that of large roots, and resultantly, they may carry a lot more nutrients and metabolites. These features make them favorite places for microbial colonizers. Interestingly, fine roots also showed higher bacterial OTU

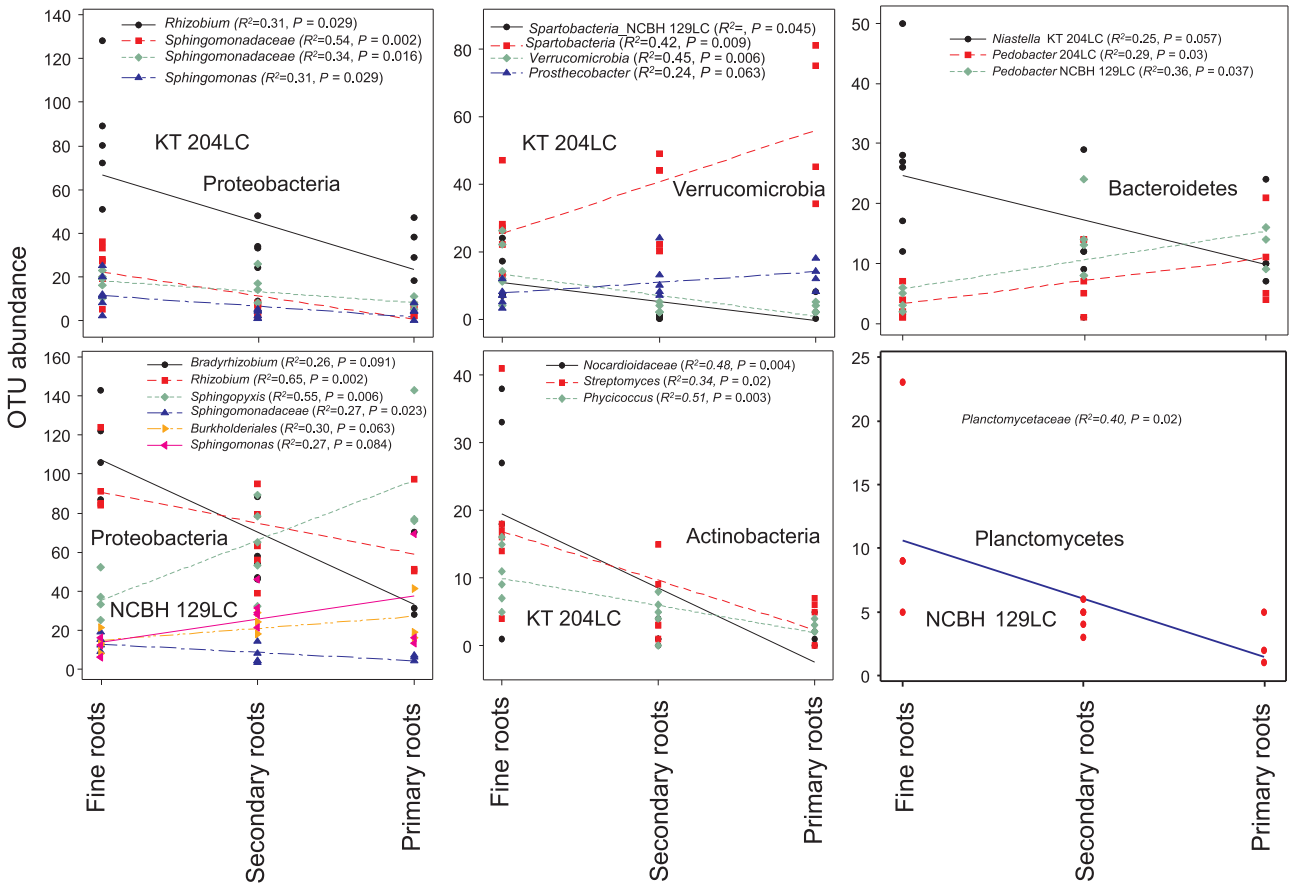

Fig. 2. Abundance of specialist OTUs across the root phenotypic trait gradient. Although OTUs from various phyla of two nicotiana cultivars (NCBH 129LC and KT 204LC) are plotted separately (e.g. *Proteobacteria*), yet in some cases of other phyla, these are plotted in the same panel and labelled accordingly. To do so, we plotted OTUs belonging to genera (Rhizobium), families (Sphingomonadaceae), classes (Spartobacteria) and phyla (Verrucomicrobia) in one comparison. The ANOVA with a linear fitting on the means was conducted to test the effect of root phenotypic trait gradient on bacterial OTU abundance. The figure was re-drafted from the data, with permission (Saleem et al., 2016).

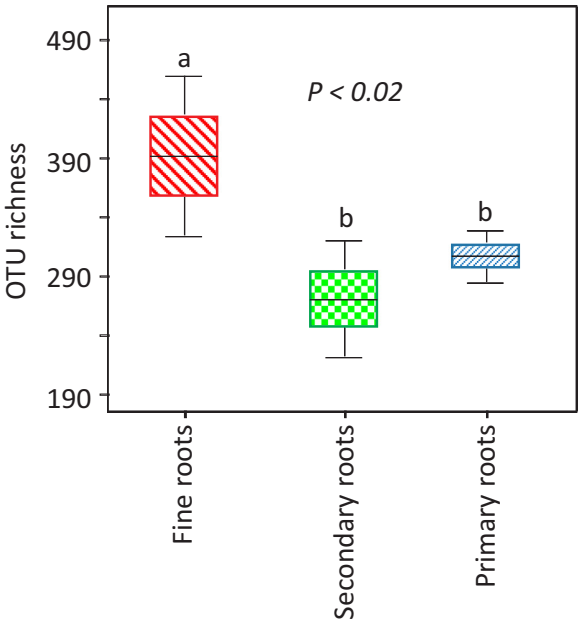

Fig. 3. Impact of root phenotypic trait gradient on root-inhabiting bacterial diversity. Fine roots showed higher microbial species richness than the secondary or primary roots of the field-grown nicotiana plants, implying that plants with many fine or root hairs may produce more exudates, and thus may recruit relatively diverse microbial species for mutualistic benefits. The significant differences among treatments were determined by ANOVA followed by Tukey's test. Error bars represent means ± 1SE.

richness (Fig. 3), partly implying that the plants with relatively more fine roots (or root hairs) may recruit highly diverse microbial communities for mutualistic benefits. Second, fine root specialists are (might be) passive colonizers who didn't enthusiastically colonize roots but got established there due to some stochastic processes (e.g., wounding on root hairs) (Gaiero et al., 2013). Moreover, the lower diversity and abundance of specialists than generalists (Fig. 2) may be due to a lack of cellular machinery in these bacteria that determine their potential to colonize woody phenotypic traits (Gaiero et al., 2013; Hardoim et al., 2008). Meantime, the higher relative abundance of some OTUs from root hairs to primary roots reflected their potential to colonize the woody roots.

Regarding the impact of root phenotypic traits on rhizosphere microbiome, Pérez-Jaramillo et al., (2017) developed an interesting analogy between root phenotypic traits and rhizosphere microbiome. They linked the abundance of *Bacteroidetes* to thin and thick root phenotypes (Pérez-Jaramillo et al., 2017). While referring to human microbiome research in which Bacteroidetes show high relative abundance in the gut of lean and weight loss animal hosts (mice, human hosts) (Brown et al., 2012; Filippo et al., 2010; Pérez-Jaramillo et al., 2017), they reported a greater abundance of Bacteroidetes in the rhizosphere of thin rooting wild bean accessions. Conversely, Actinobacteria and Proteobacteria showed a high relative abundance in the rhizosphere of thick rooting bean accessions, thus making an analogy of lean vs obese beans like animal hosts (Pérez-Jaramillo et al., 2017). On the contrary, we didn't see any difference in Bacteroidetes abundance in the rhizosphere of two nicotiana cultivars; though abundance of some OTUs differed across root phenotypic traits (Fig. 2) (Saleem et al., 2016). Nevertheless, several studies have also shown a significant abundance of

Bacteroidetes in the rhizosphere microbiome of the commodity crops, their wild relatives, and other plant species (Ji et al., 2017; Jorquera et al., 2016; Lundberg et al., 2012; Mahoney et al., 2017). Moreover, they also showed the depletion and enrichment of several OTUs in the rhizosphere of various bean accessions that suggest a potential impact of root phenotypic traits on rhizosphere microbiome (Pérez-Jaramillo et al., 2017).

1.3. Root phenotype and genotype

There are several studies that have shown the impact of plant genotype and cultivar on root microbiome (Lundberg et al., 2012; Saleem et al., 2016). However, few studies have demonstrated that phenotypic traits potentially influence root and rhizosphere microbiome (Pérez-Jaramillo et al., 2017; Saleem et al., 2016). We suggest that root phenotypic traits or architecture may influence the recruitment and colonization of microbes depending, among others, on their cell wall structures, metabolic profiles, surface area, edaphic properties, biotic and abiotic stress conditions (Figs. 1 and 3). Meantime, it is also important to understand and link together the genetic, environmental, and crop management factors that determine the root system and its traits including microbial component.

1.4. Key determinants of root system architecture

Apart from plant genetics, a number of crop management and environmental factors regulate the growth, development, and penetration of roots in the soil profile. Owing to a tremendous phenotypic plasticity, the root system responses to edaphic factors vary largely depending on soil physiochemical properties and plant types. For instance, soil physical than chemical properties had more impact on root elongation in cereals (Bengough et al., 2011; Rogers et al., 2016). While in general, the soil compaction causes irregular root growth (shorter, thicker), shape (bell, tortuous), and distribution in the agroforestry, agronomic and horticultural plants (Alameda and Villar, 2009; Grzesiak et al., 2013; Tracy et al., 2013). But the moderate bulk density improves root growth in the nutrient-rich loamy soils (Tracy et al., 2013). Similarly, soil texture (relative proportion of sand, silt, and clay) also influences root phenes by regulating oxygen, water, and nutrients supply to the roots (Rich and Watt, 2013; Rogers et al., 2016; Tracy et al., 2013). The coarse than fine-textured soils induce more lateral roots in plants (Gruber et al., 2013). Likewise, the excess and deficiency of each macro- and micro-nutrient induce particular changes in root phenes, and the responses may be root trait specific. For instance, lateral rather than primary roots are more sensitive to nitrogen supply in the soil (Tian et al., 2014). A recent study investigated the impact of 32 binary combinations of N, P, K, S, and light on root system in *Arabidopsis thaliana*. The P application caused the most significant single-nutrient effects whereas the N-responses were light dependent. But the effects of K and S on the root system depended on their combinations with other nutrients (Kellermeier et al., 2014).

In addition to these, several environmental factors such as drought, temperature, precipitation, greenhouse gases (i.e., CO_2), and climate change also influence the root traits, and the details about these factors are not the center of this article. Meanwhile, soil biodiversity (i.e., nematodes, protists, bacteria, fungi, phages) and its ecological interactions with plants could potentially impact root system and its traits. In this regard, the role of different mycorrhizal species in influencing the root phenes by their growth-promoting properties is studied under normal and stress conditions (Yang et al., 2015). Meanwhile, the bacterial effects on root phenes are mostly investigated under the influence of individual or consortia of few species (e.g. Egamberdieva et al., 2016; Patten and Glick, 2002). However, improvement in root system as a function of microbiome species diversity needs to be studied (Saleem et al., 2018). Nevertheless, intensive theory-theory research is needed to discern the reciprocal interactions between root phenes, rhizosphere biota, edaphic properties, and agronomic practices.

2. Concluding remarks

Finally, we conclude by presenting some important questions that may include but are not limited to these, and indeed merit future research investigation. What are the eco-evolutionary mechanisms that determine the generalist or specialist behavior of microbial taxa across root phenotypic trait gradient? What are the fitness costs and trade-offs underlying the selection of generalists and specialists in the root system? What could be the responses of generalists and specialists to root phenology and phenotypic plasticity across domestication and environmental gradients? What is the ecological and genetic basis of functional overlap in microbial taxa across different root traits? Do the root phenotypic traits differ in their metabolomic profiles, physical structures, anatomy and other biological properties that eventually determine microbial niche breadth in the rhizosphere and root system? How do microbial networking and co-metabolism during cell wall degradation determine the microbial succession and composition in the roots? How do the plant life trait history (e.g. monocots vs dicots, fast vs slow growing, etc.) impact the root system architecture, microbiome, and soil health indicators? What are the impacts of agronomic and soil management practices on root system architecture and microbiome in a climate change scenario? How can we develop integrated crop breeding approaches to improve belowground root traits and biota to increase crop production and farm economy? Simply saying, linking rhizospheric interactions to root phenology, architecture, biochemistry, and anatomy may help us preserve below ground resources for maintenance and enhancement of natural and agroecosystem services in the context of climate and use change.

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